Agren, G.I. (ed.) 1984
State and Change in Forest Ecosystems -
Indicators in Current Research
Swed. Univ. Agric. Sci.
Dept Ecology & Environmental Research
Report nr 13, pp. 111-119.

FOREST GROWTH AND NUTRIENT DYNAMICS

Göran I. Agren

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Abstract

In this paper I suggest a representation of a forest in terms of its content of biomass (carbon) and nitrogen. The forest is viewed as consisting of two subsystems, trees and soil, where the former immobilizes carbon and nitrogen and latter mineralizes them. These processes can be formalized in the following way:

- Production of new leaves is proportional to the amount of nitrogen in them. The proportionality constant is the nitrogen productivity.
- Production of other tissue is a function of the amount of leaves.
- Weight loss of litter follows for a given age class of litter an exponential decay curve. The decay rate varies between different types of litter.
- Nitrogen concentration in a given age-class of litter is a linear funtion of the weight loss of the litter. The slope of the function can be calculated from the decay rate of the litter.

With this representation it is possible to estimate the effect of a series of perturbations of the forest.

INTRODUCTION

An important criterion when choosing a representation of a system is that it can be done with as few qualitatively different processes as possible. When applied, it reduces the number of different mental images of the system that has to be handled simultaneously, thus making it easier for us to interpret changes in the system under different conditions. In this paper, I will propose a representation of forest ecosystems that satisfies this criterion. This representation is of course, not the only one possible, but in addition to satisfy the simplicty criterion, it is also one where most of the processes are reasonably well understood and parameterized.

First of all, the forest ecosystem is a dual system of production and decomposition, systems which I henceforth will refer to as vegetation and soil, although part of the decomposition might take place well above-ground in e.g. dead branches. Each of these two subsystems will be described by their content of carbon (biomass) and nitrogen. The concentration of the interest to nitrogen derives from the recognition of nitrogen as one of the most critical elements in limiting growth (Cole and Rapp 1981, Vitousek 1982). We have also convenient ways of formulating the dynamic interactions between nitrogen and carbon in the subsystems. In situations where nitrogen is not limiting (nitrogen saturation), the representation to be presented here is still applicable. However, it will mainly present a static situation unless the system is perturbed, when relaxation to steady state again can be predicted. Particularly in situations where phosphorous deficiency is the main growth limitation, it is possible that the representation proposed here should apply directly with only nitrogen exchanged everywhere against phosphorous (cf. Berendse and Bosatta, in prep.).

The time scale I want to consider in this paper is one of hundreds of years. As a consequence, I will be satisfied with a time resolution of one year (two orders of magnitude smaller) - within-year dynamics is per se not of interest in this context. This has considerable consequences for the formulation of the processes we want to take into account as well as for our possibilities of deriving these processes at all.

A combination of all the above considerations leads to a conceptual model as shown in Figure 1. This figure demonstrates the three dimensions of decomposition of the forest ecosystem. It has the division into vegetation and soil, into carbon and nitrogen, and into components representing different time constants. This break-down is perhaps not exactely the one to be used in a realization of the model (woody components might perhaps have to be further subdivided etc.) but it displays the important qualities that I think must be taken into account. I have in another context strongly argued against the use of complicated models and the model proposed here looks, indeed, quite complicated (Ågren 1981). However, in the rest of this paper I will demonstrate that although at a first appearance the model might look complicated it is, actually, based upon only a few critical processes. I will also show that we, in general, have a good understanding of these processes and propose specific formulations of them.

CARBON IN VEGETATION

In my view, the most important production process is the one of production of leaves, because the entry of inorganic carbon to the organic pool of carbon in the ecosystem is through the leaves. Hence, the total fixation of carbon must be strongly related to the amount of leaves in the ecosystem. Also, of the above-ground components of the vegetation the leaves have the most rapid turn-over and should therefore be the component most susceptible to perturbations of the ecosystem. As I have demonstrated earlier, the production of leaves, at least in coniferous forests, can be calculated from their content of nitrogen with the aid of the nitrogen productivity concept (Ågren 1983ab).

Production of other tissue than leaves could be calculated from the amount of leaves. O'Neill and DeAngelis (1981) demonstrated this for boreal gymnosperm forests. Very high correlations between above-ground production and leaf area index in Scots pine and Norway spruce forests have also been reported (Albrektson et al. 1977). The changes in the relative distribution between above- and below-ground components with different availability to nitrogen could be related to the nitrogen concentration in the leaves (e.g. Ingestad 1979).

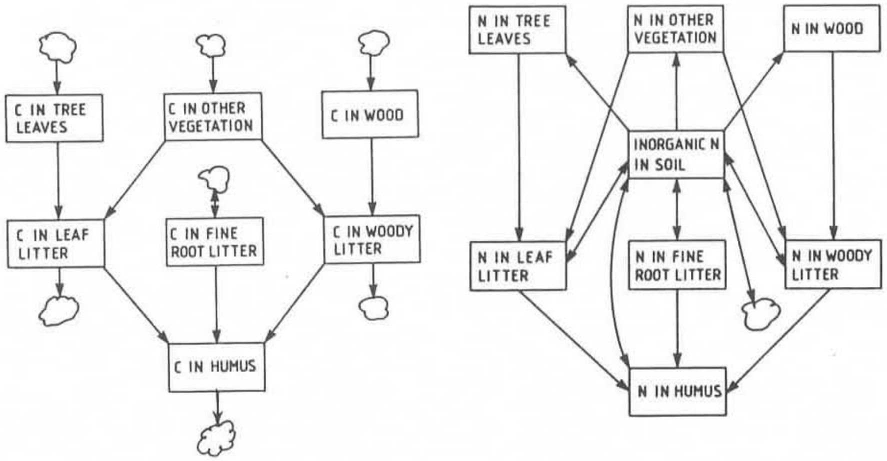

Figure 1. Principal structure of a model of carbon-nitrogen interactions in forest ecosystems. Only qualitatively different components are shown. Certain fractions like wood and litter might have to be further subdivided in practical applications.

Production of litter is a process that has high variability in time, but at least for the litter types with slow decay, rates of input of fresh litter represents only a small fraction of the litter present in the soil. Therefore, from the point of view of the soil the short-term variation in litter production should in most cases be possible to neglect. Also, the fraction of carbon lost from the vegetation as litter should generally represent only a small fraction of the total content. I therefore suggest that litter production, with the exception of fine roots, is taken as proportional to the corresponding vegetation component and with a constant proportionality constant. If one wants to study more dramatic events in the forest as severe droughts or insect outbreaks it is, of course, necessary to modify this assumption.

If we let W be the amount of leaf biomass, N the amount of nitrogen in the same leaf biomass, and V the amount of woody components, then, the turn-over of carbon in the vegetation can be summarized in the following equations:

$$\frac{dW}{dt} = (a - bW) N - fW \qquad (1)$$

$$\frac{dV}{dt} = rW - sV \qquad (2)$$

where a, b, f, r, and s are parameters. The expression (a-bW) is the nitrogen productivity (Ågren 1983ab).

NITROGEN IN VEGETATION

The uptake of mineral nitrogen from the soil solution by the vegetation is probably complete (Ingestad 1982). Our task in this context is therefore to calculate the net mineralization rate of nitrogen in the soil. However, there is a problem of partitioning the mineralized nitrogen between different types of vegetation. One simple solution is to let the partitioning be in proportion to the leaf biomasses of the different types of vegetation (cf. Ingestad et al. 1981). This is probably a too simplistic view as different plant species do not have the same ratios of leaf biomass to fine roots. This problem can be avoided by just treating grown-up and well-stocked forests where the trees dominate the nitrogen uptake.

The amount of nitrogen fixed in the woody tissue should be proportional to the production of these components. The proportionality constant is probably a function of the age or some other characteristic showing the developmental stage of the forest (Ovington 1959), but could perhaps in a first approximation be set constant.

Losses of nitrogen from the vegetation to the soil must follow the loss of carbon. The concentration of nitrogen in fresh woody litter ought to be the same as in the corresponding biomass. Nitrogen in the leaves, on the other hand, is to a large extent retained by the vegetation. It is not well known how the concentration of nitrogen in fresh leaf litter varies with nitrogen concentration in the living leaves, but there are suggestions that the concentration in the fresh litter is independent of the living leaves (Aronsson, pers. comm.).

Let N_v be the amount of nitrogen in the woody components. The turn-over of nitrogen can then be described by

$$\frac{dN}{dt} = \text{uptake} - pfW \qquad (3)$$

$$\frac{dN_v}{dt} = h(rW - sV) \qquad (4)$$

where p and h are parameters. The formulation of the uptake needs further specifications.

CARBON IN SOIL

As a coarse description of the carbon (weight) loss of litter most authors seem to agree that a negative exponential function may be used (e.g. Meentemeyer 1978, Swift et al. 1979, Melillo et al. 1982) but with different decay constants for different types of litter. More refined analyses will require more complicated functions, for example a sum of two negative exponentials or even more complicated functions (Lousier and Parkinson 1976, Carpenter 1982; although certain derivations in the latter reference are not correct). Bosatta and Staaf (1982) show that the negative exponential can be derived from a simple model of substrate-microorganism interaction if it can be assumed that the production of microbial biomass is proportional to the amount of carbon in the substrate.

Even if it thus is possible to formulate the loss of carbon from a substrate in a simple manner we have not solved the problem of carbon turn-over in the soil. The loss of carbon from a given substrate is not equivalent to its loss from the system. Part of it is certainly lost as CO_2 but another part is transformed into other types of substrate. This transformation is a process which we lack understanding of. For the time being I content myself with letting these transformed carbon compounds become something defined as humus. The humus is therefore something that might require further qualifications in qualities. Carpenter (1981) has attempted to formulate this process in general terms.

Let C be the amount of carbon in any of the different soil carbon fractions. The turn-over of soil carbon is then formulated as

$$\frac{dC}{dt} = \text{input} - kC \qquad (5)$$

where k is a parameter characteristic of that particular type of substrate. The parameter k has been related to nitrogen and ligning concentration in the substrate (Meentemeyer 1978, Aber and Melillo 1982, Melillo et al. 1982). The input to the soil carbon fractions consists either of fresh litter, in which case the formulations have been given above or of transformed soil carbon in which case we presently have no valid formulation of the process.

NITROGEN IN SOIL

The typical pattern of changes in nitrogen content of a decomposing substrate is a small initial decrease followed by an increase over one to several years up to a level higher than the initial one and finally a decrease in the nitrogen content (e.g. Staaf and Berg 1977). Such a behaviour is consistent with the model developed by Bosatta and Staaf (1982) (see also Parnas 1975). This model predicts that with M equal to the amount of nitrogen in the soil substrate

$$\frac{M}{C} = \frac{M_o}{C_o} + \left(\frac{f_N}{f_C} - \frac{M_o}{C_o}\right)\{1 - (C/C_o)^x\} \qquad (6)$$

where

$$x = \frac{\varepsilon}{1 - \varepsilon}$$

M_o and C_o are the initial amounts of nitrogen and carbon in the substrate, respectively, and f_N f_C and microbial parameters describing their nitrogen concentration, carbon concentration and efficiency in carbon utilization, respectively.

In the special case of $\varepsilon = 0.5$, Eq. (6) simplifies to a linear relationship between nitrogen concentration in the substrate and the weight loss of the substrate, which can be written

$$\frac{M}{C} = \frac{M_o}{C_o} + g(1 - C/C_o) \qquad (7)$$

where g is a parameter. Eq. (7) has been tested on large number of litter types by Aber and Melillo (1980, 1982) with good agreement. Moreover, the parameter g in Eq. (7) can be coupled to the decay rate of carbon, k. (Bosatta and Staaf 1982) such that

$$g = a_o + a_1 k \qquad (8)$$

where a_o and a_1 are parameters. Hence, the description of the decomposition of a given substrate can be done using only one parameter, k.

DISCUSSION

In the preceding sections I have discussed how different processes in a forest ecosystem can be described in terms of their carbon and nitrogen turn-over. It is now time to step back to see whether these processes form a complete description and whether the description satisfies the criterion of being "simple". I think that it is fair to say that the simplicity criterion is satisfied. The vegetation processes go essentially back to the production of leaves and the understanding of this process through the nitrogen productivity concept seems satisfactory. Decomposition of a given substrate in the soil can be done with a single parameter, and there seems to be no reason to treat different litter types qualitatively different. Within this frame-work it is only their rate constants that differ - a quantitative difference.

The weaknesses of the proposed representation lies in the parts that we at present do not know how to give a satisfactory formulation. The most important ones are the following:

Which subdivisions of substrate in the soil are necessary? Or in other words, how long does a given litter quantity behave independently of other soil organic matter? To some extent this is a practical question of just book-keeping several litter cohorts, but there is also the principle question of when for example fungal mycelia connect different litter cohorts such that they effectively behave as one single substrate. Related to this is the question of humus formation. Is it reasonable to assume that when a substrate is losing weight a fraction of that loss represent a transfer of the substrate into humus, and if so, will that fraction be changing drastically during the decomposition process? Aber and Melillo (1982) suggested in a model that one should stop treating the different litter cohorts separately at the time when they start a net mineralisation of nitrogen and from then on lump them together as humus. To me this seems too early a time as the weight loss of a substrate continues with the same rate long after the net mineralisation has started, and, at least with leaf litter, this decay rate is much higher than that of humus.

The competition for nitrogen between different types of vegetation seems a difficult process to formulate on secure grounds. One can circumvent this problem by restricting the analysis to only monospecies forests. However, this excludes the early developmental stages of the forest as well as interesting competition problems between tree species, e.g. when will the forest be a spruce forest and when will it be a pine forest, or can the two species coexist.

Climatic variables have so far not been mentioned in this discussion. The most important effects of climate in this representation is on the decomposition rates. As Ågren (1983a) has shown, the nitrogen productivity seems relatively independent of site conditions and hence different climates. The direct effects of climate on the vegetation processes should therefore not be very important. Indirectly, the climate will influence the vegetation through the changes in availability of nitrogen. There seem to be fairly good possibilities of including climatic effects on the decomposition rate. Meentemeyer (1978) and Berg et al. (1983) have discussed different ways of coupling decomposition rate to precipitation and temperature on a yearly basis. More detailed analysis with higher time resolution are also possible (Bosatta et al. 1980), but pertain to another level of models.

The analysis of the representation presented is under way. Parts of the model presented have, however, already been analysed. Ingestad et al. (1981) used the leaf part of the vegetation and a considerably simplified version of the soil component to study effects of nitrogen fertilisation in coniferous forests obtaining possible fertilisation regimes. Ågren (1983c) used the same model to estimate the magnitude of the impact of certain effects of acid rain on Scots pine and Norway spruce forests. One result of which was that the internal cycling of nitrogen is an efficient buffer against changes in the mineralization rate of soil nitrogen. Another use of the very same model has been a study of stability properties of coniferous forests, showing that there exists no simple relationship between fertility and stability and that different measures of stability give very different results (Ågren 1983d). Also the soil system is buffered against changes in the decomposition rate as a consequence of Eq.(8). The implication is that a decreased decomposition rate decreases not only the mineralization rate but also the competitivity of the microrganisms for mineralized nitrogen, hence leaving a larger share to the vegetation. Thus, if for example acid rain would lower the microbial activity, the nitrogen uptake by the vegetation might still be more or less the same (Bosatta 1982).

REFERENCES

Aber, J. D. and Melillo, J. M., 1980. Litter decomposition: Measuring the relative contributions of organic matter and nitrogen to forest soils. Can. J. Bot., 58: 416-421.

Aber, J. D. and Melillo, J. M., 1982. FORTNITE: A computer model of organic matter and nitrogen dynamics in forest ecosystems. College of Agricultural and Life Sciences, University of Wisconsin-Madison, Res. Bull. R3130.

Ågren, G. I., 1981. Problems involved in modelling tree growth., Stud. For. Suec., 160: 7-18.

Ågren, G. I., 1983a. Nitrogen productivity in some conifers. Can. J. For. Res., 13: 494-500.

Ågren, G. I., 1983b. The concept of nitrogen productivity in forest growth modelling. Mitteilungen der Forstlichen Bundesversuchsanstalt, 147: 199-210.

Ågren, G. I., 1983c. Model analysis of some consequences of acid precipitation on forest growth. In: Ecological effects of acid deposition. National Swedish Environment Protection Board - Report PM 1636: 233-244.

Ågren, G. I., 1983d. Model analysis of some stability properties of northern coniferous forests. Lesovedenye (in press).

Albrektson, A., Aronsson, A. and Tamm, C. O., 1977. The effect of forest fertilisation on primary production and nutrient cycling in the forest ecosystem. Silva Fenn., 11: 233-239.

Berendse, F. and Bosatta, E., 1983. A step towards a theory of decomposition in nutrient-poor ecosystems. Submitted.

Berg, B., Jansson, P. E. and Meentemeyer, V., 1983. Litter decomposition - Regional and local models. This volume.

Bosatta, E., 1982. Acidification and release of nutrients from organic matter - A model analysis. Oecologia (Berl.), 55: 30-33.

Bosatta, E. and Staaf, H., 1982. The control of nitrogen turn-over in forest litter. Oikos, 39: 143-151.

Bosatta, E., Bringmark, L. and Staaf, H., 1980. Nitrogen transformations in a Scots pine forest mor - model analysis of mineralization, uptake by roots and leaching. In: Persson, T. (ed.), Structure and function of northern coniferous forests - An ecosystem study. Ecol. Bull. (Stockholm), 32: 565-589.

Carpenter, S.R. 1981. Decay of heterogenous detritus: A general model. J. theor. Biol., 89: 539-547.

Carpenter, S. R., 1982. Comparisons of equations for decay of leaf litter in tree-hole ecosystems. Oikos, 39: 17-22.

Cole, D.W. and Rapp, M., 1981. Elemental cycling in forest ecosystems. In: Reichle, D.E. (ed.) Dynamic properties of forest ecosystems (International Biological Programme; 23), Cambridge University Press, pp. 341-409.

Ingestad, T., 1979. Nitrogen stress in birch seedlings. II. N, K, P, Ca, and Mg nutrition. Physiol Plant., 45:149-157.

Ingestad, T., 1982. Relative addition rate and external concentration; Driving variables used in plant nutrition research. Plant, Cell and Environm., 5: 443-453.

Ingestad, T., Aronsson, A. and Agren, G. I., 1981. Nutrient flux density model of mineral nutrition in conifer ecosystems. Stud. For. Suec., 160: 61-71.

Lousier, J. D. and Parkinson, D., 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot., 54: 419-436.

Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. Ecology, 59: 465-472.

Melillo, J. M., Aber, J. D. and Muratore, J. F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology, 63: 621-626.

O'Neill, R. V. and DeAngelis, D. L., 1981 Comparative productivity and biomass relations of forest ecosystems. In: Reichle, D. E. (ed.) Dynamic properties of forest ecosystems (International Biological Programme; 23), Cambridge University Press, pp. 341-409.

Ovington, J. D., 1959. Mineral content of plantations of Pinus sylvestris L.. Ann. Bot., 23:75-88.

Parnas, H., 1975. Model for decomposition of organic material by microorganisms. Soil Biol. Biochem., 7: 161-169.

Staaf, H. and Berg, B., 1977. Mobilization of plant nutrients in a Scots pine forest mor in Central Sweden. Silva Fenn., 11: 210-217.

Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in terrestrial ecosystems (Studies in ecology, Vol. 5). Blackwell Scientific Publications.

Vitousek, P., 1982. Nutrient cycling and nutrient use efficiency. Am. Nat. 119: 553-572

Presented at the ESF Workshop "What properties of a forest ecosystem give the best information on state and change", March 21-24, 1983, Uppsala, Sweden.